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VISION WITH CONTROLLED MOVEMENTS OF THE RETINAL IMAGE

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Previous work on eye movements (Lord & Wright, 1950; Ratliff & Riggs, 1950; Barlow, 1952; Ditchburn & Ginsborg, 1953; Riggs, 1958) has shown that when a subject fixates as steadily as possible upon a well-defined target, certain involuntary eye-rotations persist.

The natural involuntary movements of the eye include (i) a high frequency *tremor* of amplitude less than 0·5 minute of arc (min.arc) and frequencies up to 150 c/s, (ii) intermittent rapid *flicks* of up to 50 min.arc occurring at irregular intervals (from 0·03 to 5 sec), and (iii) a slow motion *drift* at the rate of about 1 min.arc/sec in the interflick periods.

It is convenient to use a common measure for rotations of the eye, size and motion of the target and for movements of the retinal image. This is obtained by referring them all to equivalent angles in the visual field. The minute of arc is taken as the unit angle, the second being used only as a unit of time. At the fovea, 1 min.arc corresponds to a distance of about 5μ; the distance between the centres of adjacent cones is about 0·6 min.arc.

The fact that these involuntary movements exist does not prove that they have any important function in visual perception. However, by means of a device previously described (Ditchburn & Fender, 1955) it is possible to produce a visual target which moves so that its image remains on the same part of the retina despite involuntary eye movements. We call this a *stabilized retinal image*. When the subject views a stabilized image, perception of detail fails intermittently. For example a black bar a few min.arc wide on a circular field 60 min.arc in diameter (in the centre of the fovea) and 50 m-L brightness would be seen easily and continuously in normal vision. However, when the image is stabilized the bar appears to fade out leaving the whole field uniformly illuminated; the bar reappears after a short interval and then disappears again, the whole process of 'fade-out' followed by spontaneous regeneration being repeated at irregular intervals with a median time of about 5 sec for the subject used in the experiments reported below.

Eye tremor causes the image to move across the retina so that the edges of a pattern (for example, the edges of the black bar) are scanned across certain retinal receptors which are therefore subjected to rapid changes of illumination. Marshall & Talbot (1942) suggested that these changes generate 'on' and 'off' responses in the nerve pathways associated with the stimulated retinal receptors. They showed that many experimental results could be included in a theory of this type. Ditchburn (1955) discussed the effect of eye movements as a whole, taking into account the results of some early experiments with the stabilized image. He attributed the impairment of vision with the stabilized image to the loss of some of the information derived from the on–off signals.

If this theory is correct, it should be possible to improve vision with the stabilized retinal image by introducing controlled movements of the retinal image. Experiments of this type are reported in a later section of this paper. Vision should also be restored by using intermittent illumination of the stabilized retinal image, and this effect has also been observed (Ditchburn & Fender, 1955).

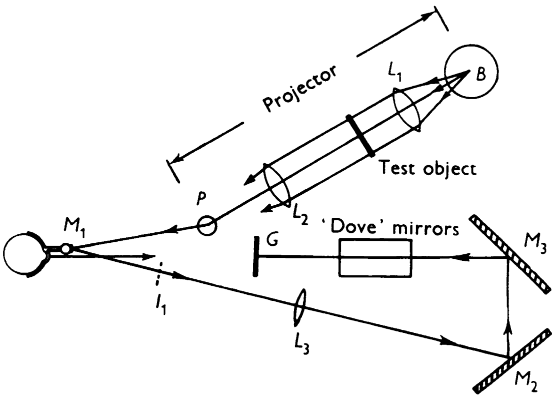

Fig. 1. Apparatus for producing a stabilized retinal image. For explanation see Text.

METHODS

Stabilization apparatus

The apparatus shown in Fig. 1 can be used for producing a stabilized image and was described in detail by Ditchburn & Fender (1955). For convenience its operation is now summarized before describing the modifications needed to give controlled movements of the retinal image. Light from the ball B of a 'Pointolite' lamp is rendered parallel by the lens L_1 and illuminates the test object. The lens L_2 focuses the source on the mirror M_1 and forms an image of the test object at I_1. For convenience, the projector system is above the plane of the diagram and the beam is brought into the plane by a periscope P. The lens L_3 forms an image of I_1 on the ground-glass screen G by reflexions at the mirrors M_2 and M_3, and the subject views this screen directly. The lens L_3 reverses the direction of motion of the image with respect to the eye, but this is corrected horizontally by the pair of mirrors M_2 and M_3 and vertically by a mirror analogue of a Dove prism. The magnification of the optical system may be adjusted so that the angular movement of the image on the ground-glass screen is the same as the angle of rotation of the eyeball, and thus the retinal image is stationary with respect to the retinal receptors.

Apparatus for producing controlled movements of the retinal image

The natural movements of the retinal image derived from eye movements having been annulled by stabilization, it is possible to introduce retinal image movements which are controlled by the experimenter and not by the voluntary or involuntary eye movements of the subject. The modifications needed for this purpose will now be described.

Simulation of drift. The effect of the natural drift movement may be simulated by giving the retinal image an oscillatory movement of large amplitude and of period comparable with the mean time between flicks in normal vision. The apparatus shown in Fig. 1 was modified in the following way. The mirror M_2 was carried on a pivoted mount; a small metal bellows (sealed at normal air pressure) was placed behind the mirror and was connected by a length of flexible plastic tubing to a larger bellows which could be deformed by a crank arm driven by an electric motor mounted independently on the floor. The eccentricity of the crank could be varied, thus altering the displacement of the large bellows. The pressure generated deformed the small bellows slightly and this displacement was used to rotate the mirror M_2 through a small angle about the vertical axis. In this way the image on the screen G was given a motion additional to the movements which produced stabilization, thus producing a slow movement of the retinal image in the horizontal direction with respect to the retinal receptors. The target used for this work was a fine vertical black line on a bright circular field 60 min. arc in diameter. The two bellows joined by small-bore tube form a filter system which rejects any high frequency vibrations generated by the motor and its gearing.

Simulation of flick and tremor. The apparatus used for introducing flick movements and for simulating a high frequency tremor is an adaptation of the Eindhoven string galvanometer. A fine wire which passes between the poles of a strong magnet is used to form the vertical black line in the test object of the stabilizing system shown in Fig. 1.

If the wire is connected to a battery through a resistance and a key, then a rapid movement of the wire is produced by closing the key, and the displacement may be adjusted by altering the resistance. In the experiments on simulated flicks the motion of the wire was critically damped so that there was no overshoot of the image as there is in a natural flick. The movement took place in about a millisecond, that is, more rapidly than in a natural flick.

If alternating current is passed through the wire then oscillatory movements are produced. In order to have available frequencies down to 4 c/s, the alternating current is generated by a bar magnet rotating between coils. This magnet is carried on the spindle of a small servomotor which also drives a chopper disk. A beam of light passes through the disk into a photo-electric cell, the amplified output of which is applied to the input terminals of a frequency meter; the frequency of rotation of the magnet and hence the frequency of vibration of the line can thus be read directly. The movement of the wire was recorded photographically on a magnified scale; the movement was found to be sinusoidal and the amplitude was obtained from the record.

Experiments have been performed using vibrations as small as 0·05 min. arc in amplitude. Measurements on movements of this magnitude can give significant results only when stringent anti-vibration precautions have been taken. The apparatus is therefore mounted on a massive table made of well-seasoned oak, the table being firmly fixed to a bitumastic floor. Components which must be shielded from vibration are attached rigidly to the table, using kinematic constraints where possible. Those pieces of the apparatus which might cause vibration, electric motors, chopper disks, electro-magnetic shutters, are mounted elastically and where possible on individual supports fixed to the floor.

Reduction of results. It is necessary to have a criterion for assessing the loss of vision due to stabilization. We define the visibility factor V thus:

$$V = \frac{\text{Time for which the image is seen clearly}}{\text{Total time of observation}}.$$

The time of observation is 60 sec. This period is long compared with the median time of alternation of 5 sec for the visibility of a stabilized image, but it is not so long as to fatigue the subject unduly.

In all tests of visual performance, especially near a threshold, it is found that there is a day-to-day variation in the subject's response even when the experimental conditions are maintained constant. In the present series of experiments this appears as a variation in the visibility factor as defined above. If however we measure alternately the visibility factor with no imposed movement and the visibility factor with an imposed movement, the experimental conditions for each measurement being maintained constant, then we find that these vary together. A reduction formula can thus be used to eliminate the variation of the visibility factor with no imposed movement in comparing the effects of different imposed movements.

Moreover, it simplifies the presentation of the results if the formula is used to reduce the results obtained for certain standard visual conditions to standard numbers; that is, complete visibility of the image is to be represented by unity, total disappearance by zero and the visibility of a stabilized image with no imposed movement by some fixed number within this range. The formula which we use is:

$$V_R = V_M\left\{1 + \frac{(1 - V_M)}{(1 - V_0)} \cdot \frac{(V_s - V_0)}{V_0}\right\},$$

where V_M is the measured visibility factor with imposed movement;

V_0 is the mean of two measurements of the visibility factor (without imposed movements) made immediately before and after the measurement of V_M;

V_s is the mean value of V_0 over the whole series of experiments; and

V_R is the reduced value of V_M which we take as the measure of the efficiency of vision with imposed movement.

A reduction process of this type is suitable only for a restricted variation of V_0. For tremor and drift we use it to reduce values of V_0 between 0·21 and 0·60 to a standard value of $V_s = 0·37$.

Reproducibility of observations. Viewing the stabilized image makes fairly severe demands on the subject and reports become irregular if periods of observation are prolonged beyond about half an hour. It is therefore not possible to derive the standard deviation for each individual point by repeating each observation a large number of times, but a number of selected conditions were repeated up to ten times. For example in a series of experiments in which the line vibrated 0·86 min.arc at 20 c/s, the result was $V_R = 0·37$ with a standard deviation for the mean value of 0·03.

The reliability of individual points is assessed by subdividing the 60 sec period into three intervals each of 20 sec and determining the mean deviation of the three results. This deviation is found to correlate fairly well with the deviation of the individual value from the group mean in those tests which were repeated a number of times. In the diagrams which follow, black circles represent observations whose mean deviation is $\leqslant 0·06$, open circles represent those whose mean deviation is $> 0·06$ but $\leqslant 0·15$. When the mean deviation exceeds 0·15 the observation is rejected.

RESULTS

Imposed drift (or low-frequency oscillation)

Experiments have been performed with a constant frequency of 0·55 c/s, but with various amplitudes. The target was a vertical black line 5 min.arc wide across a circular patch 60 min.arc in diameter and 15 mL brightness. Values of V_R for various drift amplitudes are shown in Fig. 2. It will be seen that although V_R rises as the amplitude is increased, no significant increase has occurred at the median drift amplitude of normal vision. We conclude that the normal median drift by itself cannot prevent 'fade-out', though the larger drifts may have some effect.

The imposed movement takes the line away from the visual axis. The subject attempts to follow the movement but the stabilization arrangements prevent him from overtaking the image. The abnormal situation created by the imposed movements was always apparent to the subject, and the large amplitude movement sometimes caused a sensation of nausea.

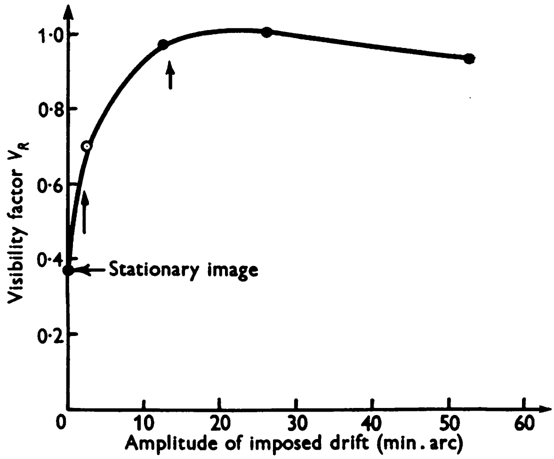

Fig. 2. Effect of imposed drift motion on the visibility of a stabilized retinal image. The small vertical arrows indicate median and maximum drift amplitude for the subject used in this work when fixating without stabilization.

Imposed flicks

Using the apparatus described above with a bar 3 min. arc in width and a field of 15 m-L brightness, the effect was studied of rapid movements with a displacement varying from 2·5 to 25 min. arc.

The value of V_R for different flick amplitudes is shown in Fig. 3. It will be seen that flicks for all values of the displacement down to the smallest tested (2·5 min. arc) produced a marked increase in V_R. The smallest flick moved the image across only four cones. Flicks of amplitude much less than that of the median flick of normal vision are sufficient to cause regeneration.

The subject reported that for all amplitudes of flick used in these trials the wire movement could be seen. Regeneration of the image always followed the flick and gave a *very sharp* image, that is, sharper than that which is normally observed after spontaneous regeneration.

Imposed tremor

A series of experiments designed to measure the effects of small tremor motions has been performed on one subject. The target was a vertical black line 2·75 min. arc wide on a circular background 60 min. arc in diameter and of 50 mL brightness. The amplitude and frequency of the motion were varied over the range 0·05–1·10 min. arc and 4–20 c/s respectively. The different amplitudes and frequencies were presented in irregular order, together with presentations of the stationary target.

Fig. 4 shows the results obtained in this series of experiments; these results are displayed as smoothed curves to clarify the figure. The consistency of the data on which these smoothed curves are based is illustrated in Fig. 5 in the case of 8 c/s and 20 c/s imposed tremor.

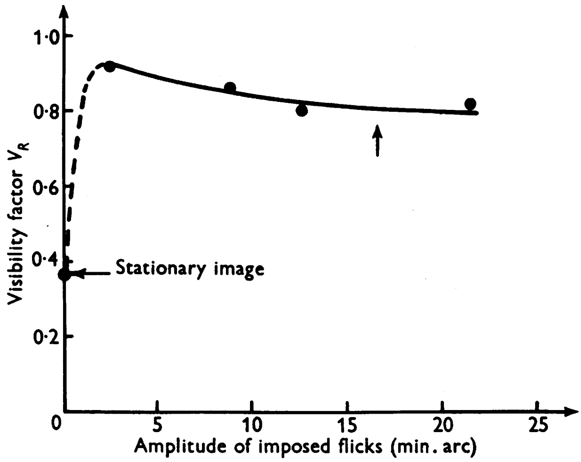

Fig. 3. Effect of imposed flick motion on the visibility of a stabilized retinal image. The small vertical arrow indicates the median flick amplitude for the subject used in this work.

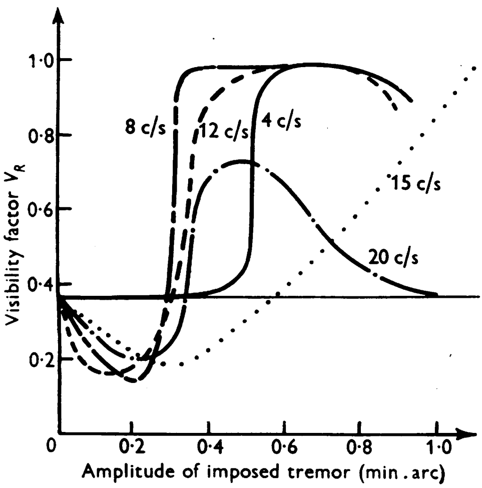

Fig. 4

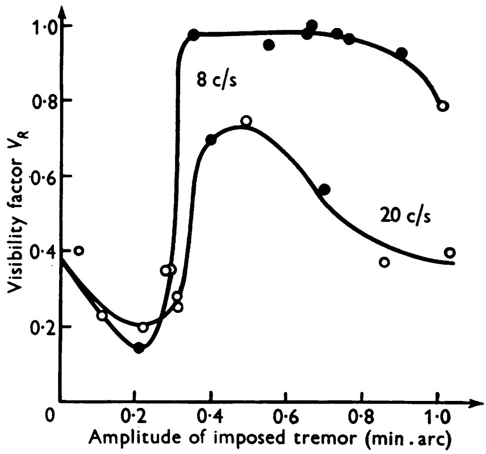

Fig. 5

Fig. 4. Effect of imposed tremor motions on the visibility of a stabilized retinal image. Smoothed constant-frequency curves.

Fig. 5. Effect of imposed tremor motions on the visibility of a stabilized retinal image. Constant-frequency curves showing experimental points.

The smoothed curves of Fig. 4 have been used to generate the contour map of visibility as a function of both amplitude and frequency of imposed tremor shown in Fig. 6. No measurements were made at frequencies below 4 c/s; this portion of the diagram is therefore conjectural and the contours are shown as dotted lines.

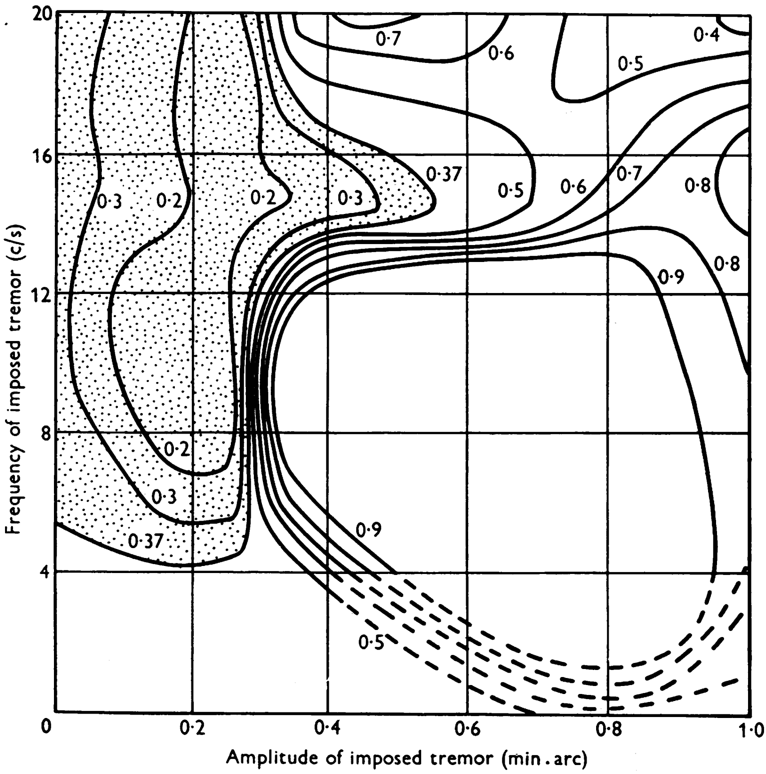

Fig. 6. Effect of imposed tremor motions on the visibility of a stabilized retinal image as a function of both amplitude and frequency. The numbers against the contours indicate the value of the visibility factor V_R.

It will be seen that for all frequencies tested, a small-amplitude tremor ($<0{\cdot}3$ min.arc) results in a depression of the level of visibility below that obtained for a stationary line in stabilized vision. At an amplitude of about 0·3 min.arc, however, there is a steep rise in visibility and the target is seen nearly all the time at amplitudes greater than this value except when the frequency is 15 c/s.

The 15 c/s curve of Fig. 4 is different from the remainder of the family and its effect is best seen on the contour diagram. Conditions of good visibility are indicated by the plateau shown in the lower right-hand quadrant of Fig. 6; in this region the value of V_R exceeds 0·90. The poor visibility region is a valley (shaded in the diagram) running right through the frequency range from 4 to 20 c/s for amplitudes smaller than 0·3 min. arc. At 15 c/s, however, this valley turns and cuts into the good-visibility plateau as far as 0·6 min. arc.

A slight fall in visibility occurs at amplitudes of about 1·0 min. arc. For displacements as large as this, however, those retinal receptors which would normally lie along the centre of the retinal image of the black line receive an exposure to light at each extremity of the image motion. Frequency doubling thus begins to occur for some receptors at this amplitude and this changes the experimental conditions.

DISCUSSION

The eye movements present during normal fixation are a mixture of drift, flick and tremor motions. In the experiments reported here each type of retinal image motion has been introduced separately, and we have sought the conditions which produce $V_R = 1$. In the following discussion we describe this condition as 'normal vision' but it should be remembered that this really means 'the target line was seen all the time'. In normal vision the eye can do much better than this; for example, at the brightnesses used in these experiments a black line less than 1 min. arc wide can be seen clearly all the time by the subject.

Imposed drifts were found to restore the visibility of a stabilized image to normality only when they were comparable in extent with the largest drifts observed in normal vision. A histogram of drift amplitudes shows a very skewed distribution with the small drifts predominating. A drift large enough to maintain normal vision is therefore a rare occurrence, and if we postulate that eye movements play an essential part in preserving visual acuity and contrast discrimination, then the normal drift component of eye movements can make only a small contribution.

The results of the experiments on imposed flicks suggest that this motion alone is capable of supporting normal vision. This, however, must be accepted with some caution, for the experiment was performed in such a way that an imposed flick was generated immediately the image appeared to 'fade-out'; thus if a flick produces any regeneration of the image at all, this experiment will tend to indicate full visibility. The significant finding from this experiment is thought to be that any flick down to the smallest tested (4 cone-diameters) produced an immediate sharp regeneration of the image which then tended to fade out again.

The perception of a stabilized image with no imposed movement goes through one complete cycle of good visibility followed by 'fade-out' and then regeneration in a median time of 5 sec. The visibility factor for such an image is about $V_R = 0{\cdot}40$, indicating that the image is seen for 2 sec out of the 5 sec cycle. During this 2 sec period the image is first seen clearly, then the boundaries become fuzzy and finally the image appears to fade into a field of uniform illumination. Only when all this has happened is the image reported as no longer seen. The median interflick period for the subject used in this work is 1·0 sec; this is an appreciable fraction of the time for which an image is seen in stabilized vision, hence if flicks alone are responsible for maintaining visual acuity it would be expected that this subject would see some of the regime of 'fade-out' even in normal vision. This is not the case, hence we must conclude that although flicks may well play an important part in sustaining vision, some additional mechanism must be operative.

It is very attractive to ascribe this role to the tremor motion of the eye; as will be seen from the 'good visibility' plateau of Fig. 6 there is an extensive choice of frequency and amplitude pairs which support normal vision. The use of an oscillatory motion instead of an impulsive one as in the flick would also appear to be an economical way of maintaining the level of visibility. The normal tremor of the eye is rather irregular but a preliminary Fourier analysis shows it to be a continuous spectrum of frequencies running from 1 c/s up to 150 c/s (which is the resolution limit of the instrument). However, the amplitude associated with any particular frequency of normal eye movements tends to lie outside the plateau region of Fig. 6; indeed many of the normal components are in the depressed region below 0·3 min.arc amplitude. Fig. 6 shows the efficacy of any one component of specific amplitude and frequency acting alone, whereas all possible components are present simultaneously in normal eye movements. The contributions from the separate components are undoubtedly additive, but so far we have no information on this matter. We see then that tremor could be used by the eye to maintain visual acuity only if there is a summation of effects over the whole frequency spectrum of eye movements.

The decrease which occurs in the visibility of a stabilized image with an imposed tremor of small amplitude may provide evidence for the interplay between steady-state signals and on-off signals in the perception of detail. When viewing a stabilized image with no imposed movement there can be no on-off signals generated by retinal image movements, and the visual acuity which remains may be ascribed to steady-state signals in the nervous pathways. If the vertical line of the stabilized image is given a small amplitude tremor motion then the average illumination falling on receptors along the boundaries of the line will be changed and this may decrease the perception of the boundaries unless the on-off signals which are now generated act in the opposite sense. In the tremor experiments reported above it is noticeable that a very steep rise in visibility occurs for amplitudes exceeding 0·3 min.arc; this corresponds to a displacement of 0·6 min.arc, which is roughly equal to the intercone spacing. It would thus appear that at the level of illumination used in these experiments (50 mL) the on-off response predominates only when the cone receives a complete exposure. This effect is practically independent of frequency.

Considering the results reported in this paper as a whole it is obvious that no single component of normal eye movements is capable of maintaining critical vision when acting alone. If normal eye movements are to be capable of maintaining clear vision this capacity must depend upon additive interplay between the different components.

SUMMARY

1. Retinal image movement is annulled by means of an apparatus which produces a visual target which moves so that its image remains on the same part of the retina despite movements of the eye.

2. It is found that imposed motion similar to the drift component of normal eye movements has little effect in preventing the 'fade-out' which occurs with a stabilized image.

3. Imposed motion similar to a natural flick produces a very sharp regeneration of the image which then fades out again. It is concluded that the flick motion plays a part in maintaining vision but is not the only effect operative in this respect.

4. Small amplitude imposed tremor motions also maintain vision, but the effect must rely on a summation over the whole frequency range of eye movements.

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